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The genera of Arundinoideae (Gramineae) in the southeastern United States

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THE GENERA OF ARUNDINOIDEAE (GRAMINEAE) IN THE SOUTHEASTERN UNITED STATES[1, 2]

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Subfamily ARUNDINOIDEAE Tateoka, Jour. Jap. Bot. **32:** 277. 1957, "Arundoideae."

Perennial or annual, small to very large herbaceous plants of wetlands, woodlands, and lowland and montane grasslands [semideserts]. Rhizomes often present. Stems erect or spreading (stolons sometimes present); nodes solid,

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[2]The illustrations (by Karen Stoutsenberger from dissections by Carroll Wood) are rearrangements of parts of FIGURES 3, 5, and 7 in C. S. Campbell's account of the family Gramineae, its subfamilies, and tribes in the southeastern United States (Jour. Arnold Arb. **66:** 123–199. 1985).

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glabrous, pubescent, or puberulent. Leaves several, basal and cauline, or cauline only; sheath margin open; blade linear to narrowly lanceolate; bundle sheaths double; chlorenchyma not radiate (except in *Aristida* and *Neyraudia*); silica bodies of various shapes, longitudinally oriented; stomata not dominating intercostal zones, subsidiary cells domed. Inflorescences terminal or terminal and axillary (axillary cleistogamous ones wholly enclosed within sheaths in *Danthonia* and *Nassella*). Spikelets few to very numerous, laterally flattened to subcylindrical, 1- to several-flowered; articulation above the glumes. Glumes 2, subequal to decidedly unequal, lanceolate, equaling or shorter than the lemmas; lemmas conduplicate, involute, or convolute, membranaceous (or indurate). Paleas shorter and narrower than the lemmas. Lodicules [3] 2 (or lacking), oblong or obtruncate, entire or shallowly emarginate, the margin sometimes ciliate. Stamens 1 or 3; filaments slender; anthers ellipsoid to linear. Ovaries ellipsoid to cylindrical. Fruit a caryopsis [achene], cylindrical or flattened, more or less clasped by persistent lemma and palea. Pericarp adnate to [free from] the seed. Hilum ovate-oblong to linear. Base chromosome numbers 9, 10, 11, 12. (Including Aristideae C. E. Hubb., Centothecoideae Soderstrom, Danthonieae Zotov, Stipeae Dumort.) TYPE GENUS: *Arundo* L.

A subfamily of about 60 genera and some 1400 species, in five tribes, distributed worldwide but with the greatest diversity, both in species and genera, in the Temperate Zone of the Southern Hemisphere. The Arundinoideae are represented in the Southeast by seven genera in four tribes (Aristideae C. E. Hubb., Arundineae Dumort., Centotheceae Ridley, Stipeae Dumort.) and a total of 43 species, half of them in *Aristida* L.

The circumscription of the subfamily has undergone numerous modifications and is accepted here in the sense of Campbell and Davidse and colleagues to include the Centotheceae, and in the sense of Barkworth & Everett to include the Stipeae, which were treated as an unplaced tribe by Campbell. Narrower circumscriptions have been proposed by Clayton & Renvoize, Conert (1987), and Renvoize (1982).

In an extensive cluster analysis using 71 characters, Renvoize (1982) demonstrated the importance of leaf-blade anatomy in defining a core group of genera. Several genera, such as *Neyraudia* Hooker f., combine features of the Arundinoideae with those of other traditional subfamilies. In a phylogenetic analysis of the family, Kellogg & Campbell concluded that the subfamily is polyphyletic and probably consists of several groups that are basal to other major clades (i.e., subfamilies) of the grasses.

Danthonia DC. and its allies were included in the Aveneae Dumort. (Pooideae) by Bentham (1883) and Hitchcock (1951) because of their glumes about as long as the spikelets, their several florets per spikelet, and their twisted geniculate lemma awns. Various studies (summarized by Campbell) have pointed out differences between the avenoids and the danthonioids in cytology, leaf anatomy, and embryology. The danthonioids were first accorded tribal status by Zotov, and their similarity to the arundinoids has since been further demonstrated by Hilu & Wright (1982) and Renvoize (1982).

The reed grasses, *Gynerium* Beauv., *Phragmites* Adanson, and *Thysanolaena*

Nees, have chlorenchyma cells with invaginated walls, a bambusoid feature. *Neyraudia* has radiate chlorenchyma (possibly C_4) and is similar and transitional to the Chloridoideae. However, it lacks other chloridoid features such as egg-shaped microhairs, cruciform silica bodies, and triangular subsidiary cells. It has slender arundinoid microhairs, but its embryo is eragrostoid. Its resemblance to *Arundo* and *Phragmites* seems to be due to convergent evolution of habit, not taxonomic affinity (Clayton & Renvoize). The presence of kranz anatomy suggests that species of *Neyraudia* are C_4, but biochemical and isotopic studies have not yet been conducted to confirm this.

Cortaderia Stapf is a danthonioid genus of about 24 species, with greatest diversity in the Andean and Pampan regions of South America. There are also four species in New Zealand and one in New Guinea. *Cortaderia Selloana* (Schultes) Ascherson & Graebner, pampas grass, is cultivated as an ornamental in warm regions of the United States. Evidence that it spreads from cultivation is lacking, although plants persisting after cultivation have been reported from North Carolina (Radford *et al.*) and Texas (Gould). In California, it is a non-spreading and popular cultivated species. Another cultivated species, *C. jubata* (Lem.) Stapf ("C. atacamensis"), a South American native, is an invasive weed along the California coast (Cowan). In California, only carpellate plants are known and abundant seed is produced apomictically (Costas Lippmann, 1977). It is also a bad weed in New Zealand (Knowles & Ecroyd).

Another danthonioid genus, *Schismus* Beauv., is represented in the southwestern United States and adjacent Mexico by two Eurasian adventives, *S. barbatus* (L.) Thell. (Gould & Moran) and *S. arabicus* Nees.

The Aristideae, the only largely C_4 tribe of the Arundinoideae, include just three genera: *Aristida, Sartidia* De Winter, and *Stipagrostis* Nees. It is distinctive both in spikelet morphology and leaf-blade anatomy (Renvoize, 1986). Anatomically, the inner layer of cells in the two-layered bundle sheaths is as large as or larger than the outer layer. The three genera can also be distinguished anatomically. In *Sartidia* the chlorenchyma is not radiate and the photosynthetic pathway is C_3. *Stipagrostis* (sometimes included in *Aristida*) and *Aristida* are both C_4 genera. In *Stipagrostis* there are no chloroplasts in the inner layer, while in *Aristida* they are present.

The unigeneric tribe Micraireae Pilger is endemic to northern Australia (Clayton & Renvoize; Lazarides). There are 13 species of *Micraira* F. Mueller, all of which grow in very thin soil and show an adaptation to this habitat condition in their ability to recover from extreme desiccation. The genus is unique in the family in having spiral phyllotaxy. The base chromosome number is 10.

The monotypic tribe Thysanolaeneae C. E. Hubb. includes only *Thysanolaena maxima* (Roxb.) O. Kuntze, $2n = 24$, of tropical southern and southeastern Asia. The genus is related to *Phragmites* and may not warrant tribal status (Clayton & Renvoize).

The Centotheceae are a small group of 11 genera and 26 species (ca. 30, *fide* Clayton & Renvoize; Tenório). Except for *Chasmanthium* Link, which is endemic to southeastern North America, and *Gouldochloa* Valdés, Morden, & Hatch, endemic to northeastern Mexico, they are pantropic. Centothecoids are similar to the herbaceous bambusoids in habit but are decidedly arundinoid

in leaf anatomy. The distinctive embryos have a mesocotyl, lack an epiblast (present in other arundinoids), and have a scutellum cleft and a rolled first leaf. Centothecoid grasses were first accorded taxonomic notice as a subtribe of the Festuceae (= Poeae) by Bentham (1883). They were subsequently treated as subfam. Centothecoideae (Clayton & Renvoize; Soderstrom; Tenório) but are here considered to be a tribe of the Arundinoideae following Campbell and Davidse and colleagues. A strongly papillate abaxial surface (absent in other grasses) characterizes all genera (Davidse *et al.*). The spikelets are strongly laterally compressed, the caryopsis is laterally flattened, and the hilum is basal and punctiform to shortly linear. Many genera have pulvinate petiolate leaves (*Chasmanthium* and *Gouldochloa* are exceptions), double bundle sheaths, and leaf tissue differentiated into palisade and spongy layers (in grasses otherwise known only in *Laciasis* (Griseb.) Hitchc., Panicoideae A. Br.). Bicellular, often filiform microhairs are commonly present (Davidse *et al.*). A base chromosome number of 12 characterizes nearly all cytologically known genera.

The only large genus, *Zeugites* R. Br., is confined to the New World tropics, as are *Calderonella* Soderstrom & Decker and *Pohlidium* Davidse, Soderstrom, & Ellis. In the Old World tropics are *Bromuniola* Stapf & Hubb., *Centotheca* Desv., *Chevalierella* A. Camus, *Lophatherum* Brongn., and the most primitive genus, *Megastachya* Beauv. Only *Orthoclada* Beauv. has representatives in both the Old World and the New. Tenório proposed (but did not validly publish) a monotypic genus for the African species of *Orthoclada*.

The Stipeae are here included in the Arundinoideae, as has been suggested by Barkworth & Everett and Watson and colleagues. However, Kellogg & Campbell hypothesized that the Stipeae form a clade that is the sister group of the Pooideae. Their amino-acid profiles are intermediate between those of the pooids and the bambusoids. Two-celled microhairs are absent from the Stipeae, as they are from the Pooideae. However, single-celled microhairs, called "pylidial hairs" by Renvoize (1985), are present in some species of *Stipa* and *Oryzopsis* sensu lato. These hairs may have evolved from the two-celled, fingerlike microhairs of Bambusoideae. In the Southeast the Stipeae are represented by two genera, *Nassella* (Trin.) Desv. and *Piptochaetium* J. Presl, each of which has been included in *Stipa* by some workers.

The stipoid genus *Oryzopsis* Michx. (including *Piptatherum* Beauv.) is represented by ten or more species in North America, mostly in the West. Three species, *O. asperifolia* Michx., *O. canadensis* (Poiret) Torrey, and *O. racemosa* (J. E. Sm.) Ricker, reach their southern range limits in the mountains of West Virginia and may yet be found in the mountains of North Carolina and Tennessee. The western species *O. hymenoides* (Roemer & Schultes) Ricker, $2n = 48$, comes eastward to Manitoba, Kansas, and western Texas and might be expected as an adventive or waif in Arkansas or Louisiana.

Although the genus *Milium* L. was included in the Stipeae by Clayton & Renvoize, who made the amazing statement that it is merely an awnless version of *Oryzopsis*, it was excluded from the tribe by Barkworth & Everett. According to anatomical data provided by Renvoize (1985), *Milium* is anomalous in the Stipeae in having tapering long cells and in lacking short cells in the leaf epidermis. It is typically pooid in its leaf anatomy, amino-acid profile, susceptibility to rusts, and cytology (see Barkworth & Everett for references).

Haustorial synergids, an unusual micromorphological feature not otherwise known in the grasses, have been found in *Chionochloa* Zotov, *Cortaderia, Danthonia* (including *Rytidosperma* Steudel), *Erythranthera* Zotov, *Lamprothyrsus* Pilger, *Pyrrhanthera* Zotov, and *Sieglingia* Bernh. (Philipson & Connor). These massive synergids extend through the micropyle to lie between the ovule and the ovary wall. Normal pyriform synergids, the typical graminoid condition, characterize *Arundo* and *Phragmites*. The ovary in *A. Donax* L. has an unusually long stalk (Bhanwra). The outer epidermal cells of the ovary accumulate an unidentified darkly staining material in *A. Donax* and *P. Karka* (Retz.) Trin. ex Steudel (Bhanwra). Intercalary growth of the chalaza after fertilization characterizes all arundinoid grasses investigated.

Information on the reproductive biology of the arundinoid grasses is incomplete. Most genera have perfect flowers. Species of *Cortaderia* and *Lamprothyrsus* are gynodioecious. The Neotropical *Gynerium sagittatum* (Aublet) Beauv., the only species of the genus, is dioecious. Self-compatibility is known in some species of *Aristida, Chasmanthium, Chionochloa, Cortaderia, Danthonia* (including some species assigned to the segregate *Rytidosperma*), *Nassella,* and *Stipa. Phragmites australis* is apparently self-incompatible. Apomixis is reported from *Cortaderia jubata* (Philipson, 1978). Four genera in our area (*Aristida, Chasmanthium, Danthonia,* and *Nassella*) produce cleistogamous as well as chasmogamous spikelets in at least one species. In most genera (all those in the Southeast) the pericarp is fused to the seed coat (ordinary grass caryopsis). However, in several (none in the Southeast) the pericarp is free or separable and the fruit is thus an achene. The genera with achenes are *Amphipogon* R. Br. (Australia), *Anisopogon* R. Br. (Australia), *Dregeochloa* Conert (southern Africa), *Elytrophorus* Beauv. (tropical Africa, India, Australia), *Hakonechloa* Honda (Japan), *Pentameris* Beauv. (southern Africa), *Pyrrhanthera* (New Zealand), and *Urochlaena* Nees (southern Africa). With "reluctantly free pericarp" (Clayton & Renvoize, p. 182) are *Molinia* Schrank (temperate Eurasia) and *Tribolium* Desv. (southern Africa). Except for *Hakonechloa,* all the genera with a free pericarp are confined to the Southern Hemisphere (or to continents derived from Gondwanaland).

The dispersal mechanisms of most arundinoid grasses depend on hairs or awns. The mature spikelets of *Neyraudia* and *Phragmites* break at the joints of the fragile rachilla. The hairs of the rachilla allow the florets to be wind dispersed. The silky, clasping lemmas of *Arundo* probably serve the same function. The long, sharp awns and short, stiff callus hairs of the lemmas of *Aristida* species cause the mature spikelets to stick in fur or skin of animals and thus to be dispersed. Peart, however, examined carcasses of some 100 marsupials and found no awned diaspores in their fur, a surprising result in Australia, where both *Aristida* and *Danthonia* are diverse. African species of *Stipagrostis* have plumose awns, enabling dispersal by wind. The awns of the lemmas of *Danthonia* species are hygroscopic, twisting and coiling and moving the floret into soil crevices, where chances for its germination are improved (Peart). (The hygroscopic awn of *Piptochaetium* may function in the same way.) The long hairs of the lemmas of the Australian *D. tenuior* (Steudel) Conert collapse on drying and rehydrate on wetting, moving the diaspores across soil and into crevices (Peart).

The arundinoid grasses are little known chemically. The leaves of *Phragmites australis* contain flavonoid aglycones (chrysoeriol, isorhamnetin, luteolin, quercetin, tricin), flavonol and flavone *O*-glycosides (e.g., glucosyl-3 quercetin and glucosyl-7 tricin), and flavone *C*-glycosides (7,3′-dimethoxy-isoorientin, isoorientin, isoscoparin, swertiajaponin, swertisin). Tricin and *C*-glycoflavones are known from about 90 percent of the grasses that have been studied (Jay & Viricel). The major flavonoid components of the "flower tissue" (= spikelets?) of *P. australis* are isoswertiajaponin and swertiajaponin (Nawwar *et al.*); also noted were 3′*O*-gentiobioside and the 3′-*O*-glucoside of swertiajaponin. In addition, there are two flavonol glycosides, rhamnetin 3-*O*-rutinoside and rhamnetin 3-*O*-glucoside, a class of compounds rare in grasses. *Phragmites australis* has a minute (0.27 percent) hydrocarbon fraction and no appreciable polyisoprenes (Buchanan *et al.*). The epicuticular layer of *Chionochloa* species contains long-chain carbon compounds (alcohols, aldehydes, alkanes, esters, and fatty acids) up to 52 carbons in length (Savill *et al.*).

Numerous fungi parasitize arundinoid grasses. *Balansia hypoxylon* (Peck) Atk. (anamorph: *Ephelis borealis* Ellis & Everhart) parasitizes *Danthonia compressa* Austin, *D. sericea* Nutt., and *D. spicata* (L.) Beauv., as well as *Aristida glauca* (Nees) Walp. and three species of *Stipa*. It forms segmented sclerotia (Sprague). *Uromyces Danthoniae* McAlp. occurs on six Australian species of *Danthonia*; however, no rusts are reported from any New World species of *Danthonia*. *Puccinia invenusta* H. Sydow & P. Sydow grows on all three species of *Phragmites* in the Old World but has no other hosts. *Puccinia Magnusiana* Körn. (worldwide) and *P. Trabutii* Roum. & Sacc. (northern Africa, southern Asia) both occur on *Arundo* and *Phragmites*. *Puccinia Neyraudiae* H. Sydow & P. Sydow is reported only from *Neyraudia madagascariensis* (Kunth) Hooker f. in southern India (Cummins).

The earliest evidence of arundinoid grasses dates from the Miocene. In a fine study Thomasson (1984) demonstrated anatomical features in silicified remains from Nebraska. Fossilized florets of the extinct stipoid genus *Berriochloa* M. K. Elias were found in the abdominal cavity of a fossilized rhinoceros, *Teleoceras major* Hatcher, and provide direct evidence of grass diet in Miocene times (Voorhies & Thomasson). Quaternary remains of *Phragmites australis* from Egypt could be confidently identified because the internal and external structures of rhizomes and attached stem bases were preserved (El-Saadawi *et al.*).

Plants of the subfamily have some economic importance. None are used for grain. Stems of *Arundo* and *Phragmites* are harvested for paper pulp in Europe and Asia, and they are sometimes important for forage. *Danthonia* species are important for forage in Australia (and to a lesser extent in western North America), as are immature plants of *Aristida* in the American Southwest, but neither is important in these respects in the Southeast. *Nassella leucotricha* is an important cool-weather forage grass in Texas. *Stipa tenacissima* L. is gathered for paper pulp in Algeria and Spain (Hitchcock, 1951).

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KEY TO THE GENERA OF ARUNDINOIDEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *perennial or annual herbaceous plants of dry to wet places. Leaf blades linear to lanceolate, flat or involute. Inflorescences paniculate (rarely racemose), terminal and/or axillary. Spikelets laterally compressed or subterete. Glumes 2, conspicuous; flowers 1 to several, disarticulating above glumes; lemmas often awned.*

A. Flowers imperfect or perfect (plants gynodioecious), forming dense tussocks. ..... [*Cortaderia.*]

A. Flowers perfect (lower florets sometimes imperfect); plants rhizomatous, or loosely to densely caespitose.

B. Plants large; leaves cauline only.

C. Rachillas glabrous; lemmas pilose throughout. ..... 1. *Arundo.*

C. Rachillas pilose; lemmas glabrous or pilose on margins only.

D. External ligules a line of hairs; lateral inflorescences often present; lemmas with excurved awn. ..... 3. *Neyraudia.*

D. External ligules absent; inflorescences strictly terminal; lemmas awnless. ..... 2. *Phragmites.*

B. Plants small to medium; leaves basal and cauline.

E. Spikelets subterete, 1-flowered; lemmas indurate, involute.

F. Lemma awns 1-parted.

G. Paleas rudimentary. ..... 6. *Nassella.*

G. Paleas slightly longer than and protruding from apex of lemmas. ..... 7. *Piptochaetium.*

F. Lemma awns 3-parted. ..... 5. *Aristida.*

E. Spikelets laterally flattened, 2- to 12-flowered; lemmas membranaceous, conduplicate.

H. Glumes and spikelets about the same length; lemmas awned; caryopses subcylindrical; leaves mostly basal. ..... 4. *Danthonia.*

H. Glumes much shorter than spikelets; lemmas awnless; caryopses laterally flattened; leaves mostly cauline. ..... 8. *Chasmanthium.*

Tribe ARUNDINEAE Dumortier, Obs. Gram. Belg. 82. 1824.

1. **Arundo** Linnaeus, Sp. Pl. **1:** 81. 1753; Gen. Pl. ed. 5. 35. 1754.

Very large perennials of sunny, damp soils and shallow, fresh waters. Roots fibrous; rhizomes stout. Stems stout, solid, glabrous; nodes glabrous. Leaves several, cauline; sheath glabrous; ligule membranaceous, margin minutely ciliate; blade lanceolate, auriculate, the margin and apex scabridulous; cross veins numerous. Inflorescences single, terminal, much branched, plumose. Spikelets lanceolate; glumes 2, lanceolate, as long as the spikelets; rachilla slender, flattened, glabrous; florets [1 or] 2; lemmas lanceolate, clasping, membranaceous to firm, 5- to 9-nerved, the lower ½ pilose; paleas lanceolate, ½–⅔ as long as the lemmas, hyaline, the margin ciliate. Stamens 3; anthers linear, the apex and base of thecae divergent. Ovaries slenderly cylindrical; styles 2, free, very slender; stigmas slightly longer than styles, plumose, laterally exserted. Caryopses oblong, smooth; hilum short; embryo large. Base chromosome number 12. LECTOTYPE SPECIES: *A. Donax* L.[4] (Name from Latin word for cane.)—GIANT REED.

A genus of three species native to the Old World. *Arundo Donax* L., $2n = 110$, the only wide-ranging species, occurs from Spain to India. The other species are *A. Plinii* Turra, $2n = 72$, of the Mediterranean region, and *A. formosana* Hackel, endemic to Taiwan.

Arundo Donax is naturalized from seed of planted specimens in the southeastern and southwestern United States. I have examined specimens from Virginia, North Carolina, Florida, Louisiana, Texas, and California.

Seed set is reported to be poor in *Arundo Donax* in India because of the failure of meiosis in a majority of the ovules (Bhanwra).

The reeds for woodwind instruments are cut from the stems of *Arundo Donax* (Clayton & Renvoize). The stems are used for thatch in southern Europe, Asia, and Africa, cellulose for paper pulp, and fodder. *Arundo Donax* is also cultivated around pools and on streambanks as an ornamental.

REFERENCES:

Under subfamily references see BAILEY *et al.*; BHANWRA; CLAYTON & RENVOIZE; CONERT (1961); MUNZ; RENVOIZE (1986); TUTIN; and WALTERS *et al.*

2. **Phragmites** Adanson, Fam. Pl. **2:** 34, 559. 1763.

Tall, rhizomatous perennials of swamps, marshes, ditches, and roadsides. Roots fibrous; rhizomes stout, scaly, horizontal to oblique; long stolons often produced by terrestrial plants. Stems glabrous, often glaucous. Leaves cauline, 10–15; sheaths overlapping, with margin free for entire length, glabrous; ligule

[4]Linnaeus included six species in his diverse genus *Arundo*. The genus was typified by removal of five of these: *A. Bambos* L. to *Bambusa* ("Bambus") by Gmelin (Syst. Nat. ed. 13 **2**(1): 579. 1791); *A. Phragmites* L. to *Phragmites* by Adanson (Fam. Pl. 34, 559, 1763); *A. epigejos* L. and *A. Calamagrostis* L. to *Calamagrostis* by Adanson (*Ibid.* 31, 530); and *A. arenaria* L. to *Ammophila* by Host (Gram. Austr. **4**: 24, *pl. 41.* 1809), leaving only *A. Donax.* Linnaeus (Gen. Pl. 35. 1754) described the lemmas as pilose (valvulae . . . basi lanugo") in *Arundo,* a feature fitting only *A. Donax* among the species he included in *Arundo.*

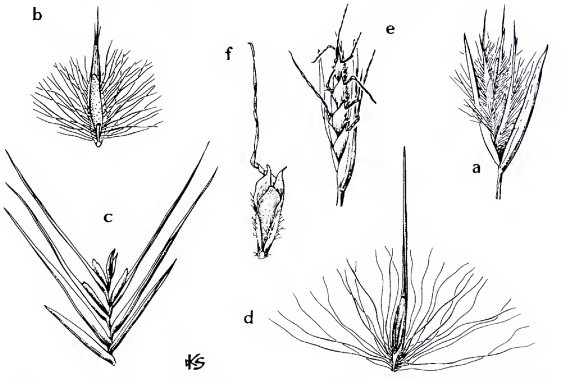

FIGURE 1. Tribe Arundineae, spikelets or their parts. a, b, *Arundo Donax*: a, spikelet, × 3; b, floret (palea and lemma enclosing flower) from adaxial side (note glabrous rachilla segment and hairs along edge of lemma), × 3. c, d, *Phragmites australis*: c, spikelet (parts spread out and hairs omitted for clarity), × 4; d, floret from adaxial side (note abundant hairs from rachilla segment), × 4. e, f, *Danthonia spicata*: e, spikelet, × 3; f, floret from adaxial side (note geniculate awn borne from middle of notch between bilobed lemma apex), × 5.

a short membrane bearing dense fringe of multicellular hairs; blades distichous below, becoming secund above, linear-lanceolate, constricted basally, widest at about ⅓ the length, tapered to a long, attenuate tip, flat, the midvein much wider and thicker than the lateral veins, cross veinlets visible on the abaxial surface. Inflorescences terminal, solitary, plumose, each node bearing several primary branches (1 or 2 of these larger than the others); nodes of the primary branches each with 1 or 2 secondary branches; secondary branches bearing single tertiary branch at each node; inflorescence axis, secondary, and tertiary branches terminated by solitary spikelets; nodes of inflorescence with ring of long, multicellular trichomes (these giving a woolly appearance to inflorescence). Spikelets numerous, lanceolate; glumes 2, unequal, the second shorter than the florets; rachilla pilose, giving the inflorescence a silky or fluffy appearance; flowers 2 to several, the lowest staminate or empty, the succeeding perfect; lemmas lanceolate, long-acuminate, 3-nerved; paleas less than ½ as long as the lemmas. Stamens 3 (lacking, 1, or 2 in lowest, staminate flower); anthers ellipsoid. Ovaries oblong; styles separate, short; stigmas plumose. Caryopses subterete, oblong; styles persistent, indurate; basal furrow broad; hilum ⅓ as long as grain. Base chromosome number 12. TYPE SPECIES: *Arundo Phragmites* L. = *P. australis* (Cav.) Trin. ex Steudel. (Name from Greek *phragmites,*

hedge, probably applied to this genus because of its dense, hedgelike growth along ditches and waterways.)—COMMON REED.

A genus of three (or more) species, nearly cosmopolitan in distribution. The only species in the New World, *Phragmites australis* (*P. communis* Trin.), is widespread, but not especially abundant or common, in the Southeast.

Occurring on all continents except Antarctica, *Phragmites australis* may have the widest distribution of any angiosperm. It was present in the American Southwest at least 1000 years before European contact (Kane & Gross), and in southern New England at least 3000 years ago (Niering & Warren). Reported in 1843 as occasional throughout New York State (Torrey), it was not reported from Georgia or South Carolina by Elliot (1821–1824) and remained unknown in those states until the 1970's (Stalter). It is now abundant in New York, where it may be in part adventive (Mitchell). It spread rapidly on Long Island during the early twentieth century, which may be explained by the introduction of a more aggressive biotype from Europe or elsewhere. Distinctive morphotypes, presumably genetically based, have been reported from southern Louisiana (Schott & White). The complex and confused taxonomy of Old World populations makes it difficult to match the North American populations with any of the numerous European varieties and cultivated forms.

Phragmites japonicus Steudel, $2n = 48$, was recognized by Tsvelev, who distinguished it from *P. australis* by its shorter glumes and spikelets and its zigzag (not straight), elongate rhizomes. The species occurs in Japan, China, and the extreme eastern Soviet Union. *Phragmites Karka* (Retz.) Trin., $2n = 18, 36, 38, 48$, grows in tropical Africa, southeastern Asia, and northern Australia (where its distribution complements that of the more temperate *P. australis*). *Phragmites mauritianus* Kunth is found in tropical Africa and the islands of the Indian Ocean (Fanshawe). The species are barely distinguishable (Clayton & Renvoize).

There is considerable variation in the chromosome complement of *Phragmites australis*. Haslam (1972) reported diploid numbers of 36, 48, 84, and 96. Aneuploids are also reported: $2n = 42, 44, 46, 49, 50, 51, 52, 54, 56$ (Gorenflot *et al.*, 1972). In Europe tetraploids and octaploids account for most populations; hexaploids are rare, being reported from Sweden (Björk), the Mediterranean region, and Iran and Afghanistan (Bahrman & Gorenflot). In the New World hexaploids have been reported from Costa Rica (Pohl). Tetraploid and octaploid clones grow together in the Danube Delta (Bahrman & Gorenflot). No correlation between ploidy, habitat, and geography was found in a survey of 40 European populations (Raicu *et al.*). Apparently the only report from North America is $2n = 48$ from a Canadian population (Hunter).

Bahrman & Gorenflot reported variation in soluble proteins of leaves in an extensive survey of European, North African, and Central Asian populations. Principal-components analysis revealed four major groups on the basis of isozymes present. The diversity of isozymes could not be correlated with ploidal level. The greatest diversity in isozymes was found in populations in Iran and Afghanistan, while the greatest variation in chromosome number was in southern Europe. Evidently, macromolecular diversification in this species has proceeded independently from chromosomal changes.

There are numerous reports worldwide of lack of seed set in *Phragmites australis*. A complete explanation has yet to be provided, and the question offers possibilities for further research. Meiosis is regular in certain populations from France (Cartier & Lenoir). However, chromosome fragmentation during microsporogenesis was detected in populations from Ireland that failed to set seed (Curran). In populations from India, megasporogenesis was normal, but microsporogenesis was arrested at the tetrad stage, and there was no mitotic division to produce the vegetative and generative nuclei (Satyamurty & Seshavatharam). Abundant seed set has been reported in populations from Afghanistan and Iran (Bahrman & Gorenflot), South Africa (Curran), Minnesota (Harris & Marshall), and the Mackenzie District, Northwest Territories, Canada (Cody). In Swedish populations, however, reproduction by seed was limited: only 0.3–8.0 percent of the florets produced viable seed (Gustafsson & Simak). No viable fruits have been reported from Ontario populations, and reproduction there has apparently been entirely vegetative (Dore & McNeill). Self-incompatibility may account for low seed set because clonal growth has produced genetically homogeneous populations (genets).

Germination is influenced by temperature, with the rate increasing linearly from 16 to 26°C, while the number of days needed for germination decreases from 25 at 16°C to only ten at 26°C. The seeds cannot germinate under more than 5 cm of water. Seed germination is little affected by salt concentrations below one percent, reaching a limit of tolerance at two percent (Kim *et al.*) in Korean populations. Plants of *Phragmites australis* are able to grow in brackish as well as fresh water. Evidently tolerance of salinity varies widely (Hocking *et al.*): a maximum tolerance for mature plants was reported as 1.2 percent in Britain, 2.9 percent in New York, and 4.0 percent on the Red Sea coast.

For detailed reviews of the autecology and physiological ecology of *Phragmites australis*, see Haslam (1972, 1973) and Hocking and colleagues. For a popular nontechnical account of general ecology and economic importance, see Brown.

Plants of *Phragmites* are used by humans in several ways. Stems are used for basketry and thatch in several European countries, and as a source of pulp for paper production, especially in eastern Europe. Immature stems provide forage for cattle in Australia (Hocking *et al.*) and southern Africa. *Phragmites australis* is an invasive weed in the northeastern United States. The rhizomes are able to grow under pavement and cause damage by cracking and piercing it (Amano & Maki; Hocking *et al.*). Unwanted populations can be effectively removed by cutting them several times annually, particularly in midsummer when rhizome starch reserves are lowest. Dense stands provide wildlife habitat in Europe (Bibby & Lunn). Reeds are planted on recently drained lands in the Netherlands and Japan (Kamio) to remove excess water and prepare the soil for agriculture.

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3. **Neyraudia** Hooker f., Fl. Brit. India **7:** 305. 1896.

Caespitose perennials of damp, sunny places. Roots fibrous; rhizomes short, solid. Stems erect; nodes glabrous. Leaves several, cauline; sheath glabrous; ligule membranaeceous, pilose (abaxial ligule a conspicuous cartilaginous ridge, pilose, becoming glabrous with age); blade linear-lanceolate, very slightly auriculate, the margin scabridulous, the surfaces glabrous. Inflorescences terminal (and sometimes axillary also), paniculate, much branched, plumose. Spikelets oblong, 3- to 6-flowered; glumes 2, broadly lanceolate, hyaline; rachilla internodes pilose; calluses pilose; lemmas lanceolate, 3-nerved, pilose abaxially toward the edges, the apex bifid, aristate from the notch, the awn scabridulous, stiffly excurved or recurved, sometimes slightly spiraled; paleas lanceolate, hyaline, 2-nerved. Stamens 3; anthers ellipsoid. Ovaries oblong, glabrous; styles 2, free; stigmas short, feathery. Caryopses linear, subterete, slightly dorsiventrally flattened; hilum short; embryo large. Base chromosome number 10. TYPE SPECIES: *N. madagascariensis* (Kunth) Hooker f. = *N. arundinacea* (L.) Henr. (Name an anagram of *Reynaudia,* a monotypic genus of Cuban grasses.)—SILK-REED.

Two species, both endemic to the Old World tropics. One species, *Neyraudia Reynaudiana* (Kunth) Keng, $2n = 40$, silk-reed, Burma-reed, is adventive in southern Florida (Hall; Long & Lakela; several specimens, the earliest from 1930, examined from Dade County). *Neyraudia arundinacea* (L.) Henr., $2n = 40$, a native of southern Asia, has been cultivated in southern Florida (Hall) and might be anticipated as an adventive. In *N. arundinacea* the first lemma subtends a perfect flower, while in *N. Reynaudiana* it subtends a sterile one.

Leaves of *Neyraudia* have an abaxial (external) ligule, which has been overlooked by some workers. It consists of a cartilaginous ridge convergent at its ends with the adaxial ligule. The abaxial ligule is pilose at first but usually becomes glabrous as the leaf matures.

REFERENCES:

Under subfamily references see BENTHAM (1883); CLAYTON & RENVOIZE; HALL; LONG & LAKELA; and PALMER & TUCKER.

4. **Danthonia** A. P. de Candolle in Lamarck & A. P. de Candolle, Fl. Franç. ed. 3. **3:** 32. 1815, nom. cons.

Caespitose perennials. Roots fibrous or wiry. Rhizomes lacking. Stems several, unbranched, terete, more or less scabridulous, glabrous or pilose; nodes with a medial constriction. Leaves several to many, basal and cauline; sheath open, shorter than the blade, glabrous or pilose; ligule a dense fringe of short hairs; blade flat (sometimes becoming involute in age), glabrous or pilose, the margin and midvein scabridulous. Inflorescences terminal and axillary (terminal cleistogamous or chasmogamous; axillary cleistogamous, enclosed in sheath); unbranched except for 2–5 primary branches, these appressed or spreading, scabridulous. Spikelets 1–3 per branch, narrowly ellipsoid, 4- to 8-flowered; glumes 2, equal, lanceolate, (3- to) 5- to 7-nerved, acute, mucronulate, persistent; rachilla straight, glabrous; calluses pilose; lemmas elliptic,

5-nerved, pilose abaxially especially near the margin, bidentate, bearing an awn from the notch between the teeth, awn with spiraled base and straight apex (axillary florets awnless); paleas broadly elliptic. Lodicules 2 or lacking, oblong to ovate, entire or truncate. Stamens 3; anthers narrowly ellipsoid, the thecae divergent apically and basally. Ovaries ovoid; styles very short; stigmas 2, feathery. Caryopses oblong to ellipsoid, dorsiventrally flattened (the abaxial face convex, the adaxial concave), the base stipitate, the apex obtuse; embryo about ⅓ as long as endosperm. Base chromosome number 12. (*Sieglingia* Bernh., nom. rejic.; including *Rytidosperma* Steudel, *Notodanthonia* Zotov.) TYPE SPECIES: *Avena spicata* L. = *D. spicata* (L.) Roemer & Schultes, typ. cons. (Named in honor of Étienne Danthoine, early nineteenth-century French botanist.)—OAT GRASS.

A genus of about 80 species (Conert, 1987), here accepted in a broad sense to include the segregate *Rytidosperma*. *Rytidosperma* was centered in Australia and New Zealand and was treated as a genus, on shaky grounds, by Clayton & Renvoize (but not by Conert, 1987). Reviewing all species attributed to *Danthonia*, Conert found no constant feature to distinguish it from *Rytidosperma*. The patterns of lemma pubescence, often used to distinguish between the two genera, show greatest diversity in Australia. Tomlinson, in an anatomical survey of the tribe, noted that *Danthonia* and *Rytidosperma* are alike in leaf-blade anatomy but differ in lodicule morphology. In *Danthonia* the lodicules lack both macrohairs and microhairs, while in *Rytidosperma* both are present. There are 32 species in Australia (Conert, 1987; Vickery) and 16 in New Zealand. There are two endemics in the Himalayas, two species in Northeast Africa, and 18 species in South America. All the North American representatives of *Danthonia* are $2n = 36$ (Gray *et al.*).

Only three species occur in the Southeast. *Danthonia spicata* (L.) Beauv. (leaf blades involute; panicle branches erect; glumes 7–14 mm long; lemma teeth (not central awn) less than 2 mm long) is widespread, occurring from Labrador to southeastern Alaska, south to western Florida and eastern Texas, and in the mountains of New Mexico and northern California. A disjunct population occurs in Hidalgo, Mexico (Conert, 1987). Canadian populations were recognized by Fernald as var. *pinetorum* Piper, said to differ in having mostly straight (not curled) basal leaves and broader, weakly nerved glumes. Dore & McNeill, however, thought most Ontario populations belonged to the typical variety.

The second southeastern species, *Danthonia compressa* Austin (leaf blades flat; panicle branches spreading; glumes 7–14 mm long; lemma teeth about 3 mm long) occurs from southern Quebec to Ohio and south to the mountains of North Carolina and Tennessee.

The third, and probably the most abundant, southeastern species is *Danthonia sericea* Nutt. (leaves involute, generally silky-pubescent; panicle branches short, erect; glumes 12–18 mm long; longer lemmas 7–10 mm long), which occurs on the Coastal Plain and Piedmont from southern New Jersey and southern Kentucky to northern Florida and Louisiana. It consists of three races, which have been accorded varietal or specific status by some workers. The

major taxonomic problem in the southeastern taxa concerns this species and its segregate *D. sericea* subsp. *epilis* (Scribner) Blomq. (*D. epilis* Scribner; leaves glabrous), reported to be restricted to the upper Piedmont of North Carolina and Georgia. Quinn & Fairbrothers made cytological preparations from 21 populations and found no karyological differences (all were $2n = 36$). Populations of *D. sericea* subsp. *epilis* in New Jersey begin growth and flowering in response to increasing soil temperature and are day-length neutral. However, populations on granitic outcrops in Georgia have their flowering time fixed genetically (Rotsettis *et al.*) and start to flower early in the year, which may be advantageous in allowing seed set before the thin soil in which the plants typically grow dries out in the summer. Gray and colleagues also studied these two regional groups of subsp. *epilis*: populations from bogs in New Jersey lacked stomata and macrohairs on the abaxial leaf surfaces but had them on the adaxial ones, while plants from well-drained sites of the Piedmont and Coastal Plain had hairs and stomata on both surfaces. Some intermediate populations from sites that were intermittently wet had abaxial hairs and stomata, but they were more plentiful on the adaxial surface. All populations had the same chromosome number, $2n = 36$. When grown in the greenhouse, both races responded to decreasing soil moisture by reduction in the width of the stomatal aperture. There is no information on compatibility or sterility between these differentiated populations, so it seems premature to recognize them taxonomically. The potential for further research is enticing.

Five other species of *Danthonia* occur in North America. *Danthonia intermedia* Vasey is boreal and cordilleran in distribution, occurring from Newfoundland to Alaska and south to the mountains of New Mexico and northern California (Cayouette & Darbyshire). It also grows on the Kamchatka Peninsula of the eastern Soviet Union (Conert, 1987; Tsvelev). *Danthonia Parryi* Scribner of the Rocky Mountains (Alberta to Colorado) is morphologically similar and probably closely related.

The second pair of western species is characterized by few-flowered inflorescences. *Danthonia californica* Bol. has an amphitropical distribution, occurring in the West from Montana to southwestern British Columbia and south to New Mexico and California, and is also reported from Chile (Munz). Pilose plants have been segregated as var. *americana* (Scribner) Hitchc. *Danthonia unispicata* (Munro ex Thurber) Munro ex Macoun has inflorescences consisting of only one (to three) spikelet(s). Its range is similar to that of *D. californica,* and Munz considered the two species as doubtfully distinct.

The Australian *Danthonia pilosa* R. Br., $2n = 48$, is adventive in California from seed planted for forage (Hitchcock, 1951; Munz).

Baum & Findlay emphasized lodicule morphology in their revision of the Canadian species of *Danthonia.* They detected four lodicule patterns, two of which are represented in the southeastern species (lodicules were absent from both *D. sericea* and *D. spicata*; club-shaped lodicules—presumably two per floret, although they did not say so—with truncate apices characterized *D. compressa*). Thus they recognized the North American species chiefly by the lodicules, a taxonomic scheme not receiving much if any subsequent acceptance. In a second paper, Findlay & Baum described a new species, *D. cana-*

densis Findlay & Baum, which occurs across Canada and the northern United States, and which differs from *D. Parryi* in the shape of the lodicules and other quantitative characters usable only by means of principal-components analysis. Such "one-character" taxonomy is problematic in a genus beset with taxonomic difficulties (see Rotsettis *et al.*; Vickery).

A notable feature of *Danthonia* is the production of cleistogamous spikelets by some species, including the three southeastern representatives. Cleistogamy was apparently first noted in the genus by Austin, who described "spikes" on short branches wholly enclosed by upper leaf sheaths. Clay (1982) investigated the reproductive biology and population genetics of *D. spicata* in North Carolina. All plants produced both axillary (cleistogamous) and aerial ("chasmogamous"—actually cleistogamous and chasmogamous) flowers,[3] but the proportion of each kind was variable. Using vegetatively produced individuals and growing these under different conditions, Clay (1982) found that plants of the same genotype consistently produced more aerial florets in the greenhouse (40 percent) than in the field (28 percent). Larger plants produced a higher percentage of axillary florets. From genetic analysis of related individuals, he determined that 50 percent of the observed variation in production of axillary florets was genetically based and 50 percent environmentally based. Genetic differences were possibly the result of natural selection. In other natural populations the percentage of axillary florets was lower: eight or nine percent in Wyoming and zero in Michigan (Scheiner & Teeri).

Clay & Antonovics (1985b) also compared genetic variation in certain morphological characters for greenhouse- and field-grown plants of *Danthonia spicata*. They found significant genetic variation present for every character examined, both vegetative (height of flowering stem; length and width of uppermost leaf) and reproductive (number of cleistogamous flowers; length of second glume). The degree of variability among closely related individuals (plants from seeds of the same carpellate parent) suggested that the aerial florets are in part cleistogamous or self-pollinated.

The three southeastern species vary in the relative proportions of aerial and axillary florets (Clay, 1983b). *Danthonia compressa* averaged 50 percent aerial florets (minimum, 35 percent); *D. spicata* ranged from zero to 70 percent, with an average of 25 percent; and *D. sericea*, including plants assignable to *D. epilis*, averaged only five percent (maximum, ten percent). Grazing or mowing appears to favor the production of axillary florets over aerial, since such populations had the highest percentage of axillary florets.

Clay (1983b) compared the weight of diaspores (caryopsis plus clasping lemma and palea) from aerial and axillary florets in the southeastern species. In *Danthonia compressa* the average weight for both kinds was 0.80 mg, while the axillary ones were 25 percent heavier in *D. sericea* and 35 percent heavier

[3]In plants from Durham County, North Carolina, studied by Clay, all aerial florets were apparently chasmogamous. However, Clay sent seeds from his study population to Philipson, who grew them in a greenhouse in New Zealand. About half of the aerial spikelets in the resulting plants were cleistogamous (Philipson, 1986). In the discussions of genetic studies by Clay, I have used the categories aerial and axillary florets where he used "chasmogamous" and "cleistogamous." See discussion below and Philipson for further details, and see Darbyshire & Cayouette for comments.

in *D. spicata*. In the two latter species about two thirds of the difference was due to heavier lemmas and paleas in the axillary florets.

A comparison of the fitness of plants derived from aerial and axillary caryopses in *Danthonia spicata* showed only a slight difference (Clay & Antonovics, 1985a). The advantage in survival was mostly during the seed and seedling stages (Clay, 1983a). Both kinds of diaspores germinate in mid- to late spring in North Carolina. Maximum germination was about 30 percent for seeds stored dry at room temperature for several months. Axillary cleistogenes germinate over a longer period (30 percent germination in ten days) than aerial (10 to 15 percent in 30 to 40 days).

Subsequent studies by Philipson show the diversity of reproductive features in *Danthonia spicata*. She grew 49 plants (122 panicles) from a single North Carolina population and found that 52 percent of the florets from aerial panicles were in fact cleistogamous (rather than chasmogamous, as was assumed by Clay). There was wide variation in the percentage of cleistogamy, and 58 panicles (nearly 50 percent) were wholly cleistogamous. In the aerial cleistogamous florets the anthers were tiny and indehiscent; the pollen grains germinated in situ, and the tubes grew through the anther wall into the adjacent stigmas. Often, both chasmogamous and cleistogamous florets were produced in the same spikelet (the cleistogamous generally proximal to and maturing sooner than the chasmogamous). Thus, many plants produced three kinds of diaspores: chasmogamous and cleistogamous ones from aerial inflorescences, both dispersed some distance by the hygroscopic lemma awns, and atelechoric awnless axillary cleistogenes generally germinating quite close to the parent plant.

Danthonia spicata is able to grow in diverse environments, from open sandy soil in full sun to closed-canopy oak-pine forest with only ten percent of full sunlight in Michigan (Scheiner & Teeri). Individual plants have the ability to recover from severe droughts. Both genetic differentiation (microevolution or genetic drift) and phenological flexibility appear to contribute to this ecological amplitude.

Population variability based on genetics has also been demonstrated in the Australian *Danthonia caespitosa* Gaudich. (Quinn & Hodgkinson). The response to density and to temperature varied along a latitudinal gradient. The infraspecific diversity of species from different regions tends to counter the suggestion of Clayton & Renvoize that the Arundinoideae are not successful and are outside the mainstream of grass evolution.

Seed dormancy in the Australian species *Danthonia carphoides* F. Mueller ex Bentham and *D. caespitosa* was investigated by Hagon. Seeds sown within two weeks of ripening had 30 percent germination. After storage at room temperature (dry) for six weeks, all dormancy was broken. Germination responses were not appreciably affected by temperatures in the 15–35°C range.

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Tribe ARISTIDEAE C. E. Hubbard in Bor, Grasses Burma Ceylon India Pakistan, 685. 1960.

5. **Aristida** Linnaeus, Sp. Pl. **1:** 82. 1753; Gen. Pl. ed. 5. 35. 1754.

Caespitose annuals or perennials of dry soils. Roots fibrous; rhizomes short or lacking. Stems several to many, erect or slightly oblique, branched from the axils, especially in the lower portion. Leaves several, cauline and basal; sheath glabrous or pilose; ligule a short, pilose membrane; external ligule (sometimes present) a cartilaginous ridge interrupted by the midvein, bearing a row of trichomes; blade linear, about as long as the sheath [absent], involute or flat, the margin and surface scabridulous. Inflorescences paniculate, more or less open. Spikelets pedicellate, 1-flowered; glumes 2, strongly unequal to subequal, sometimes awned; lemmas lanceolate, shorter or longer than the glumes, involute [convolute], 3-nerved, calluses prominent, shortly hispid, the awn conspicuous, scabridulous [plumose], with 2 lateral teeth whose bases are sometimes fused to the lower portion of the awn forming the awn column; paleas much shorter than lemmas, 2-nerved. Lodicules 2. Stamens 3 or 1; anthers linear. Ovaries shortly cylindrical; styles 2, short; stigmas plumose, laterally exserted. Caryopses compressed or terete, tightly enclosed by lemma and palea,

FIGURE 2. Spikelets or their parts. a–d, Tribe Aristideae, *Aristida longispica* (sect. *Aristida*): a, spikelet with glumes spread apart, × 6; b, floret (lemma and palea) containing mature caryopsis, the 3-awned lemma completely enclosing palea and caryopsis, × 6; c, caryopsis, × 6; d, palea, × 12. e–h, Tribe Stipeae, *Piptochaetium avenaceum* (*Stipa avenacea*): e, spikelet with single floret (only basal portion of lemma awn shown), × 2; f, entire floret, showing relative length of hygroscopic lemma awn, × ½; g, floret (note hairy base of lemma and rachilla forming bearded, sharp-pointed callus), lemma clasping pointed palea (only base of lemma awn shown), × 5; h, palea, × 5. i–k, Tribe Centotheceae, *Chasmanthium latifolium* (*Uniola latifolia*): i, spikelet, × 1½; j, floret (lemma and palea enclosing flower), × 3; k, caryopsis, × 5.

sometimes longitudinally furrowed. Base chromosome number 11. TYPE SPECIES: *A. adscensionis* L., the only species included in the genus by Linnaeus. (Name from Latin *arista,* a beard or awn.)—THREE-AWN GRASS.

A genus of about 330 species distributed nearly throughout the tropical and warm-temperate regions of the world. Twenty species occur in the Southeast. The genus is reasonably well known, thanks to the worldwide studies of Henrard (1926; 1927; 1928; 1929; 1932; 1933a, b). A synopsis of the southeastern species (including those in Delaware, Maryland, Virginia, West Virginia, and Kentucky) has been presented by Allred (1986). His keys allow easy identification of the species in eastern North America.

The subgeneric classification of *Aristida* is confused and difficult. There are probably parallels in the evolution of spikelet characters noted by Henrard (1926; 1927; 1928; 1929; 1932; 1933a, b). Section ARISTIDA (sect. *Chaetaria* (Beauv.) Trin.) (awns of the lemma persistent) accounts for about 200 species worldwide and 18 of the 20 species in the Southeast. The section was divided by Hitchcock (1924, 1951) into informal groups, a scheme also followed by Allred (1986) and seemingly prudent in view of the lack of understanding of the phylogeny of the genus. About one third of the southeastern species are annuals (group Dichotoma of Hitchcock, 1951), the remainder perennials. A common situation in the section is pairs of intergrading species; for example, *A. basiramea* Engelm. ex Vasey and *A. dichotoma* Michx. Polyploidy characterizes several species of the southwestern United States (DeLisle, 1973) of the *A. purpurea* Nutt. complex (group Purpureae of Hitchcock, 1951). *Aristida Roemeriana* Scheele, $2n = 22$, includes only diploids; *A. longiseta* Steudel, *A. Fendleriana* Steudel, and *A. glauca* (Nees) Walp., diploids and tetraploids ($2n = 22, 44$); *A. Wrightii* Nash, diploids, tetraploids, and hexaploids; and *A. purpurea* Nutt. ($2n = 88$), octaploids as well. In none of these species were morphological criteria found to distinguish the various autopolyploids (DeLisle, 1969). The polymorphic and pantropic *A. adscencionis* L., $2n = 22$, has numerous infraspecific categories. In the New World it has been reported from Texas westward to California and southward through Central and South America.

Section ARTHRATHERUM (Beauv.) Reichenb. (awn column deciduous at its base) is most diverse in Africa. There are only two species in the Southeast. *Aristida desmantha* Trin. & Rupr. (longer glume less than 2 cm long; awn column 2–5(–7) mm long) occurs in our area only in Arkansas and Louisiana. *Aristida tuberculosa* Nutt. (longer glume more than 2 cm long; awn column 8–15 mm long) is widespread in the eastern United States and in all of the southeastern states except Tennessee and Arkansas. Chromosome counts (e.g., *A. brevisubulata* Maire, $2n = 22$, and *A. pallida* Steudel, $2n = 44$) suggest the occurrence of polyploidy in African representatives of this section.

The chiefly African sect. PSEUDARTHRATHERUM Chiov. is not represented in the New World. This section differs from the preceding in having the awn column deciduous at its summit (i.e., just below the level at which the lateral awns branch from the central one).

Also not represented in the New World is sect. STREPTACHNE (R. Br.) Domin

(awn column present, not articulated). This section, recognized by Lazarides and by Bourreil & Reyre, was included without comment in sect. ARISTIDA by Clayton & Renvoize. One of its species, *Aristida Humbertii* Bourreil & Reyre, known from Angola, is unique in the genus in that all three awns are reduced to short mucros.

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Tribe STIPEAE Dumortier, Obs. Gram. Belg. 83. 1824.

6. **Nassella** (Trinius) Desvaux in C. Gay, Hist. Chile Bot. **6:** 263. 1854.

Caespitose perennials. Stems hispid or glabrous; nodes appressed-hispid, becoming glabrous with age (lower nodes usually geniculate). Leaves several to many, mostly basal; sheath pubescent or glabrous; ligule an unfringed membrane (abaxial ligule absent); blade setaceous to linear, more or less involute, hispid abaxially, less so adaxially. Inflorescences solitary, terminal, paniculate; branches flexuous, scabrid, sometimes hairy. Spikelets 1-flowered, slightly laterally compressed, disarticulation above glumes. Glumes 2, equal, broadly lanceolate, acute [awned], 3-(to 5-)nerved. Lemmas elliptic, convolute, becoming indurate, hispid basally, the surface densely covered with short, stout prickles (seemingly tuberculate), contracted into a smooth, basally fringed collar at the base of the awn, the awn 5–10 times longer than lemma, geniculate, scabrid, hairless. Paleas elliptic, much shorter than lemmas (or absent), nerveless, hyaline. Lodicules 2, glabrous, fleshy. Stamens 3; anthers oblong. Ovaries oblong, glabrous; styles free, stigmas 2. Caryopses oblong to pyriform, laterally compressed, smooth; hilum linear; embryo large, with epiblast. Base chromosome number 14. (*Urachne* sect. *Nassella* Trin. Mém. Acad. Sci. St. Pétersb. Sci. Nat. VI. **1:** 73. 1830.) LECTOTYPE SPECIES: *N. pungens* Desv., designated by Parodi (1947). (Origin of name unknown.)

A genus of about 50 species (Barkworth & Everett), in an area from Patagonia north through the Andes into the Caribbean region, Mexico, and the United States, and western Canada. The only southeastern representative, *Nassella leucotricha* (Trin. & Rupr.) Pohl (*Stipa leucotricha* Trin. & Rupr.), Texas wintergrass, $2n = 28$ (Gould), occurs sporadically in western Louisiana and southwestern Arkansas and ranges southward through Texas into South America. It is abundant in Texas, where it is important as a cool-season forage grass.

The caryopses of *Nassella leucotricha* have prolonged, erratic germination. They probably germinate more or less continuously throughout the year, except during lengthy dry spells (Fowler). On the basis of controlled-environment experiments, however, Call & Spoonts characterized the optimal parameters for germination and hypothesized that in central Texas most germination would occur from late September through mid-November and, during mild winters, also from December through February.

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7. **Piptochaetium** J. Presl in K. Presl, Reliq. Haenk. **1**: 222. *pl. 37*. 1830.

Caespitose perennials of dry, open places. Stems branched only near the base, glabrous; nodes glabrous, constricted medially. Leaves several per stem; sheath ribbed, glabrous; ligule longer than wide, membranaceous (abaxial ligule absent); blade linear, flat to involute, midvein prominent, surface and margin scabridulous. Inflorescences solitary, terminal, open, paniculate; branches scabridulous. Glumes 2, equal, lanceolate-acuminate, conspicuously 3- to 5-veined, margin hyaline. Spikelets solitary, 1-flowered, terete. Calluses subulate [cuneate], covered with long, stiff, extrorse hairs. Lemmas narrowly oblong [elliptic], 3-nerved (nerves visible from adaxial surface), coriaceous, often tuberculate above, margin involute, fitting into the sulcus of the palea, apex thickened, scabridulous [spiny]; awn several times longer than lemma body, spiraled (hygroscopic), scabridulous. Paleas lanceolate, slightly longer than the lemmas, sulcate medially, glabrous, the apex protruding between the lemma margins. Lodicules 3. Stamens 3; anthers narrowly ellipsoid. Ovaries cylindrical; stigmas 2, plumose. Caryopses slenderly cylindrical, firmly enclosed by palea and lemma. Base chromosome number 11. TYPE SPECIES: *P. setifolium* J. Presl, the only species. (Name from Greek *piptein,* to fall, and *chaete,* bristle, referring to the deciduous lemma awns of the type species.)—NEEDLEGRASS.

A genus of about 30 species. The circumscription follows Barkworth & Everett, and Parodi. *Piptochaetium* is distinguished from other genera of the Stipeae by its grooved palea into which the margins of the involute lemma fit (Barkworth & Everett; Parodi). It is characterized by phloem fibers in the leaf blades, colorless cells between the abaxial epidermis and the bulliform cells, and circular to paradermally rounded vascular bundles (Parodi & Freier).

Only two species are found in the Southeast. *Piptochaetium avenaceum* (L.) Parodi (*Stipa avenacea* L.), $2n = 22, 28$, occurs from Massachusetts to southwestern Ontario (Dore & McNeill) and Michigan, south to northern Florida and eastern Texas. It is known from all the Southeastern States, where it grows in oak or pine woods, along roadsides, and in fields.

Piptochaetium avenacioides (Nash) Valencia & Costas (*Stipa avenacioides* Nash) is endemic to central Florida (Hall; Hitchcock; Wunderlin). It has longer awns (6–10 cm, vs. 4–6) and longer lemmas (12–18 mm, vs. 8–10) than *P. avenaceum* (Hall). The two species are otherwise similar and perhaps closely related, but because of considerable parallelism in the Stipeae (Barkworth & Everett), this is perhaps a premature statement. The range of *P. avenacioides,* although restricted, does not appear to overlap that of *P. avenaceum.*

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Tribe CENTOTHECEAE Ridley, Mater. Fl. Malay Penin. **3**: 122. 1907.

8. **Chasmanthium** Link, Hort. Berol. **1**: 159. 1827.

Single-stemmed or loosely clustered perennials of open woods. Roots fibrous; rhizomes short, approximately horizontal. Stems unbranched or sparingly branched. Leaves cauline, several; sheath glabrous or pubescent; ligule a short hyaline membrane or fringe of hairs; blade linear to linear-lanceolate, scabridulous on veins, otherwise glabrous or sparsely pilose. Inflorescences terminal and/or axillary, open or contracted. Spikelets oblong, laterally flattened, sessile or pedicellate, 2- to 12-flowered; glumes 2, equal or subequal, deltoid to lanceolate, acute to acuminate, conduplicate, 3- to 7-nerved, the midvein often scabridulous; lemmas narrowly oblong, acuminate, acute, or bifid, 5- to 15-nerved, the midvein scabridulous or ciliate; paleas about as long as the lemmas, bicarinate, bulged out near the base, the keel scabridulous. Lodicules 2, lobed-truncate, 2- to 4-nerved. Stamens solitary; anther broadly oblong to linear. Ovaries oblong; styles short; stigmas 2, plumose. Caryopses ovoid to ellipsoid, laterally flattened, asymmetric, the apex subacute, the base cuneate to obtuse; embryo small, less than ½ the length of the grain. Base chromosome number 12. (Excluding *Gouldochloa* Valdés, Morden, & Hatch.) TYPE SPECIES: *C. gracile* Link = *C. laxum* (L.) Yates, the only species included by Link. (Name from Greek *chasma,* open or gaping, and *anthos,* flower.)

A genus of five species, all endemics of eastern North America and all occurring in the Southeast. *Chasmanthium* was long included in *Uniola* (Chloridoideae). Detailed studies by Yates established the affinities of *Chasmanthium* with the Centotheceae and the heterogeneity of *Uniola* as circumscribed by Hitchcock and other agrostologists. All species of *Chasmanthium* are self-compatible (Yates).

Chasmanthium latifolium (Michx.) Yates (large spikelets pedunculate, pendent), $2n = 48$, is the most distinctive species and presumably the least closely related to the others. It is found from New Jersey to Kansas south to the Florida Panhandle and south-central Texas, with outlying populations in central Nebraska and the mountains of northeastern Mexico.[6] It occurs in all of the

[6]Reported from Manitoba by Yates as follows: Canada, Manitoba, Cow Creek Bridge, Stillwater, *Gruver,* 13 July 1936 (NCU). I have examined the specimen, and it is *C. latifolium* as annotated by Yates. However, it is unlikely this specimen came from Manitoba. The printed heading of the label reads "Herb. of Margaret G. Dudley/Winnipeg, Canada." There is no locality called Stillwater in Manitoba. There *is* a Cow Creek Bridge in Stillwater, Payne County, Oklahoma, well within the range of *C. latifolium.* Darwin Gruver is unfamiliar as a collector of Canadian plants to the Canadian botanists with whom I have corresponded. Thus I believe the specimen in question came from Oklahoma, and *C. latifolium* should be excluded from Canada's flora.

Southeastern States. Plants produce both cleistogamous and chasmogamous florets. *Chasmanthium latifolium* is tetraploid, while the other species are diploid.

The four remaining species have more or less sessile spikelets and narrow, spikelike inflorescences. The closely related *Chasmanthium sessiliflorum* (Poiret) Yates, $2n = 24$ (southeastern Virginia to Missouri and Oklahoma, south to central Florida and eastern Texas), and *C. laxum* (L.) Yates, $2n = 24$ (southeastern New York to southeastern Virginia, Kentucky, and southeastern Missouri to central Florida and eastern Texas), are distinguished by their tiny (5–10 mm long) spikelets and purple anthers. In both species the lemma and palea spread, exposing the caryopsis at maturity; this distinguishes this species-pair from the other species of the genus, in which the caryopsis remains covered. *Chasmanthium laxum* differs from *C. sessiliflorum* only in having glabrous rather than pubescent leaf sheaths and collar.

Large sessile spikelets characterize the two remaining species, both of which have more restricted ranges than the preceding species: *Chasmanthium ornithorhynchum* (Steudel) Yates, $2n = 24$, occurs on the Gulf Coastal Plain of western Florida, southern Alabama, and southern Mississippi, to southeastern Louisiana. *Chasmanthium nitidum* (Baldwin ex Ell.) Yates, $2n = 24$, grows on the Atlantic and Gulf Costal Plain of South Carolina, southern Georgia, and central and western Florida. In both the spikelets are 7–18 mm long, and the caryopses are covered completely by the palea and lemma. *Chasmanthium nitidum* has glabrous inflorescence axils and only one sterile lemma per spikelet, while *C. ornithorhynchum* has densely pilose axils and two to four sterile lemmas.

The hybrid *Chasmanthium laxum* × *C. ornithorhynchum* is known from the Gulf Coast region of southern Mississippi (Yates). Hybrid populations are associated with both parental species and have enlarged sterile spikelets.

REFERENCES:

Under subfamily references see CLAYTON & RENVOIZE; CLEWELL; HALL; HITCHCOCK (1951); WUNDERLIN; and YATES.